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LARVAL-SEX AND HOST-SPECIES EFFECTS ON LOCATION OF ATTACHMENT SITES OF LAST-INSTAR BAGWORMS, *THYRIDOPTERYX EPHEMERAEFORMIS* (LEPIDOPTERA: PSYCHIDAE)

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Abstract.—In last-instar bagworms, *Thyridopteryx ephemeraeformis,* on the deciduous tree *Robinia pseudoacacia,* males more frequently attached their cases to leaves, and females more frequently attached their cases to branches. Both males and females more frequently attached their cases to branches, rather than leaves, of the evergreen *Pinus strobus.* Diameters of branches that bagworms used as case-attachment substrates were significantly related to bagworm sex and host species. Possible adaptive significances of these phenomena are discussed.

Key Words: Psychidae, *Thyridopteryx ephemeraeformis,* caterpillar behavior, *Juniperus virginiana, Pinus strobus, Robinia pseudoacacia*

The bagworm, *Thyridopteryx ephemeraeformis* (Haworth), is a polyphagous herbivore which usually feeds on woody plants. It occurs from the West Indies north to Vermont, Michigan, and Minnesota and west to Kansas and Texas, being most common in southeastern United States according to Davis (1964) and Longfellow (1980). Many other workers including Riley (1869), Haseman (1912), Jones (1927), Jones and Parks (1928), Barrows (1974), Barrows and Gordh (1974), Kaufmann (1968), Kulman (1965), Leonhardt et al. (1983), and Neal (1986) have increased our knowledge of bagworm biology. As background for our study, we present a brief generalized summary of bagworm biology in the United States based on these previous investigations.

In August to October, depending on locality, an inseminated female lays all of her eggs in her pupal exuviae which remain in the case that she made as a larva. Her egg-laden case hangs on her host plant over the winter, and her eggs hatch in late April to early June. First-instar larvae emerge from cases, construct conical cases of silk and plant materials around themselves, and may balloon, each by a silken thread, to a new location. Many no doubt die due to predation, landing on unsuitable hosts, and other factors. A larva that finds a suitable host passes through five to eight instars (Longfellow 1980), enlarging its case as it grows, before it pupates in late summer to early fall. Before pupation, a larva fastens the anterior end of its case to a substrate (usually a food plant), and turns 180 degrees assuming a head-down position. Pupae transform into adults in 2 to 3 weeks. Males are typical of most kinds of adult Lepidoptera in having wings, legs, compound eyes, antennae, and other adult characters. Females are essentially "egg bags" having reduced compound eyes, vestigial mouthparts and legs, and no wings or antennae. After insemination, a female lays her eggs in her pupal exuviae, and then either dies in her larval case or leaves it before dying. Most bagworms, which are not killed by *Homo sapiens* L., are killed by insect and other parasites and invertebrate and vertebrate predators before they reproduce.

Our study tests five hypotheses about case-attachment behavior of bagworm last-instar larvae on three hosts: the evergreen conifers redcedar, *Juniperus virginiana* L., and white pine, *Pinus strobus* L., and the deciduous tree black locust, *Robinia pseudoacacia* Ehrh. These hypotheses were prompted by features of bagworm biology, its host-plant architectures, and our preliminary field observations regarding case-attachment sites (Barrows 1974 and later observations). Our hypotheses are: (1) Female bagworms use branches rather than petioles as case-attachment sites on *R. pseudoacacia* (experiment 1). (2) Males use branches rather than petioles as case-attachment sites on *R. pseudoacacia* (experiment 2). (3) Females use branches rather than leaves as case-attachment sites on *P. strobus* (experiment 3). (4) Males use branches rather than leaves as case-attachment sites on *P. strobus* (experiment 4). (5) Bagworm case-attachment-site diameter on *R. pseudoacacia*, *P. strobus*, and *J. virginiana* is related to bagworm sex and host species (experiment 5).

The bagworm's range broadly overlaps those of all three of its host plants that we studied (Fernald 1950), and it can be locally common on these species. *Robinia pseudoacacia* has alternate, petiolate compound leaves from 20 to 36 cm long. *Pinus strobus* usually has leaves in fascicles of five, each 7 to 12 cm long and persistent on a branch for about 2 yr (Otis 1926, Ewers and Schmid 1981). *Juniperus virginiana* has small sessile (petioleless), 1.5–12-mm long leaves which persist on plants for 5 to 6 yr (Otis 1926). Bagworms attach their last-instar cases to branches, not individual leaves of *J. virginiana*.

Materials and Methods

Bagworms were sampled in Prince William, Fairfax, and Arlington Counties in northern Virginia in September to October 1983 and 1984 before autumn leaf fall. We measured attachment sites of bagworms, that were up to 2.3 m above the ground and on their hosts, from 25 trees of *R. pseudoacacia*, 10 trees of *P. strobus*, and 15 trees *J. virginiana*. Bagworms occurred on other parts of these trees which we did not sample. The greatest diameters of pupal-case attachment sites, which were nearly round to elliptical in cross section, were measured using Manostat® dial calipers accurate to 0.05 mm. We used data only from cases whose former occupants could be sexed with certainty. A male's case had his pupal exuviae protruding from its distal opening or was intact and empty with a distal tube with a circular cross section through which he obviously emerged. A female's case contained eggs in her pupal exuviae.

To test hypotheses 1–3, we used binomial tests (BTs) to look for possible differences between observed and expected attachment-site frequencies. We designated expected frequencies as 50% on branches and 50% on leaves because each bagworm had a hypothetical 50% chance of using one or the other substrate by chance alone. We tested hypothesis 5 by examining the 95% confidence intervals of the differences between all possible pairs of means. This method is more straightforward, gives more information (the magnitudes of differences between means and their 95% confidence intervals), and makes each pairwise comparison at an alpha level of 0.05. Commonly used simultaneous test procedures, e.g. the Duncan's multiple-range test, do not have these advantages (Jones 1984). The SAS computer package (SAS® Institute 1985) was used to perform statistical analyses.

Results and Discussion

Experiment 1.—In 1983, 88 of the 92 females collected from *R. pseudoacacia* were

Table 1. Experiment 5. Mean diameters of attachment sites of cases of six bagworm categories, their 95% confidence intervals, ranges, and sample sizes (N).

	Mean (mm)	95% CI (mm)	Range (mm)	N
Males on:				
Robinia pseudoacacia	1.46	0.08	0.75–4.50	122
Juniperus virginiana	1.70	0.10	0.95–3.60	86
Pinus strobus	2.09	0.14	0.90–4.00	69
Females on:				
Juniperus virginiana	2.42	0.06	1.20–4.90	328
Pinus strobus	2.84	0.10	1.70–5.50	171
Robinia pseudoacacia	2.93	0.10	1.65–9.05	303

on branches; four were on petioles. In 1984, 297 of the 303 females collected from *R. pseudoacacia* were on branches; 4 were on petioles. Thus, female bagworms more frequently attached their cases to branches (both years, $P < 0.0001$, BT). Luther P. Brown (personal communication), who sampled bagworms in Maryland, did not find any female cases on petioles of *R. pseudoacacia*, but he sampled in November after a substantial leaf drop could have occurred. It may be reproductively advantageous for a female last instar to attach her case to a branch, rather than to a deciduous leaf which would fall to the ground. First, this site would keep her eggs above the ground where they might have a lower probability of mammalian predation and fungus infection (Barrows 1974, Berisford and Tsao 1975, Munte 1982). Second, her choosing this site would put her first-instar offspring in a place where they can readily find food and from where they can balloon to other host plants.

Experiment 2.—In 1983, of 36 males collected from *R. pseudoacacia*, 33 were on petioles and 3 were on branches. In 1984, of 122 males, 89 were on petioles and 33 were on branches. Thus, males preferentially attached to petioles (1983, $P = 0.0003$, BT; 1984, $P < 0.0001$, BT). When we originally made our second hypothesis, we knew of no reason why males should preferentially attach to petioles rather than branches of this plant. Because males leave no eggs in their cases, it should be of no consequence to their fitnesses (measured as number of offspring) if their empty pupal cases fall to the ground with deciduous plant leaves. However, possible advantages of pupal-case attachment to petioles to male last-instars and emerging males are worthy of investigation.

Experiments 3 and 4.—In 1984, all 171 females and 86 of 89 males collected from *P. strobus* were attached to branches rather than leaves or leaf clusters. Thus, both sexes preferentially attached to branches (both sexes, $P < 0.0001$, BT). When we made our third and fourth hypotheses, we assumed that bagworms, attached to leaves or a group of leaves, would usually overwinter on their hosts because they were likely to attach to at least some leaves that would not soon dehisce. Under this hypothesis, case-attachment location on *P. strobus* should have little effect on bagworm fitnesses, but according to our results, bagworms preferred branches. Possible mechanistic explanations for this behavior include bagworms tend to attach their pupal cases to firm rod-shaped substrates rather than to more flexible single leaves or clusters of leaves, and they are repelled by stimuli from leafy areas just before attaching their pupal cases.

Experiment 5.—Data regarding bagworm sex, host, attachment-site diameters, and sample sizes are summarized in Table 1,

Table 2. Experiment 5. All pairwise comparisons of six bagworm categories indicating the differences between means and 95% confidence intervals of these differences for each pair.

	MRS[a]	MJV	MPS	FRS	FJV
MJV	0.24 ± 0.13				
MPS	0.63 ± 0.15	0.39 ± 0.16			
FRS	1.47 ± 0.12	1.23 ± 0.33	0.84 ± 0.16		
FJV	0.96 ± 0.10	0.72 ± 0.12	0.33 ± 0.14	0.51 ± 0.11	
FPS	1.38 ± 0.12	1.14 ± 0.14	0.75 ± 0.16	0.09 ± 0.13	0.42 ± 0.11

[a] MRS = males on *Robinia pseudoacacia*; MJV = males on *Juniperus virginiana*; MPS = males on *Pinus strobus*; FRS = females on *R. pseudoacacia*; FJV = females on *J. virginiana*; FPS = females on *P. strobus*. Members of all pairs are different from one another at an alpha level of 0.05 except for FRS and FPS because the 95% confidence interval of this pair's difference between means contains 0.

and pairwise comparisons of differences between means are listed in Table 2. On all three hosts, females attached their pupal cases to significantly larger-diameter branches than did males. Bagworms sampled by L. P. Brown (personal communication) behaved similarly to the ones we sampled on *R. pseudoacacia* and *J. virginiana*. This may be due to the facts that females are larger than males, and larger bagworms use larger-diameter attachment sites than do smaller ones (Brown, personal communication); and on *R. pseudoacacia*, males used petioles while females used branches. Males used a significantly different mean attachment-site diameter among all hosts, and females used a significantly different mean attachment-site diameter except between *R. pseudoacacia* and *P. strobus* (Table 2).

In conclusion, our study suggests some other directions for future investigation including: (1) behavior mechanisms that affect bagworm choice of diameters and kinds of case-attachment sites; (2) possible effects of bagworm genetics, parasites, and site availability, on this behavior; and (3) the possible relationship between male attachment-site location on *R. pseudoacacia* and parasitism in subsequent bagworm generations. Parasitized cases on leaves fall to the ground, and this possibly eliminates some parasites from bagworm populations.

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